

Sensory capabilities and food capture of two small copepods, *Paracalanus parvus* and *Pseudocalanus* sp.

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Abstract

Detection, handling, and selection of prey are key features of suspension-feeding copepods. Using high-speed video, we determined detection distances and durations of all elements of the food gathering process in two small calanoid copepods, *Paracalanus parvus* and *Pseudocalanus* sp. Animals were freely swimming and presented with various phytoplankton species with equivalent spherical diameters ranging from 7 μm to 33 μm . Prey detection occurred very close—within a few cell radii—to the second antennae (53% of the cases) or the maxilliped (42%). There was no effect of prey size on detection distance, but larger prey caused a significantly longer handling time. Post-detection processing of the cells was exceedingly fast. The time from detection to the cell being placed at the mouth lasted 35 ± 19 ms and rejection of unwanted cells 61 ± 21 ms. Grooming of antennules and carapace occurred intermittently and lasted 215–227 ms. The weak feeding current and fast response of the copepods allowed ample time for detection of cells entrained in the feeding current and no distant olfaction was observed. Modeled effect of cell size on cell surface concentration of cue chemicals show that only cells with a radius larger than ~ 15 μm may be detected chemically and that only very much larger and/or very leaky cells can be detected at distance. Copepods have elaborate and exceedingly fast handling techniques that allow effective prey detection and capture, but there is no evidence of remote chemically mediated sensing when feeding on algal cells up to a size of 35 μm .

Marine copepods play a pivotal role in marine food webs by making primary production available to higher trophic levels. They also upgrade the quality of this food by selective retention of essential elements, by modification (desaturation, chain elongation) of fatty acids (Dalsgaard et al. 2003), or by selective feeding (Alcaraz et al. 1980; Koehl and Strickler 1981). Copepods feed in one of three ways: they generate a feeding current and capture prey entrained in this current (Alcaraz et al. 1980; Koehl and Strickler 1981; Strickler 1982); they cruise through the water and capture prey that they encounter (Uttieri et al. 2008; Kjellerup and Kiørboe 2012); or they are passive ambush feeders that capture prey that pass within their sensory sphere (Jonsson and Tiselius 1990; Jiang and Paffenhöfer 2004; Kiørboe 2011). In the ambush-feeding mode, prey is perceived hydromechanically (Yen et al. 1992); whereas, feeding-current feeding and cruising copepods may perceive their prey chemically (Strickler 1982) and, hence, have the potential to select prey based on its biochemical composition. The first antennae of the copepod may also possess mixed-modality mechano-chemoreceptive setae (Lenz et al. 1996). The appendages that propel the copepod through the water or generate the feeding current all possess chemosensory ultra structures (Friedman and Strickler 1975; Paffenhöfer and Loyd 2000).

The ability to select particles based on their nutritional value requires advanced chemosensory capabilities and rapid neural responses. The further away from which a copepod can detect a potential prey, the higher the

copepod's chances of survival in a nutritionally dilute environment and the better the possibility to decide on the prey's potential value prior to capture. Hence, remote detection has been a long-debated issue in copepod sensory performance. Remote detection is not a strict definition, but pertains to distances on the order of a body length or times of hundreds of milliseconds prior to interception. Andrews (1983) suggested a mechanism by which copepods with a feeding current can detect prey at longer distance. The sphere of chemicals surrounding a prey cell deforms and elongates when the cell is within the feeding current. The leading edge of this chemical signal will then reach the copepod before the particle, thus allowing time for adjusting the feeding current toward the capture area. Jiang et al. (2002) subsequently modeled the extension of the active sphere for a number of geometries of feeding currents and swimming behaviors. They concluded that slowly cruising copepods and, in particular, copepods with a feeding current may be able to remotely detect prey particles due to a potentially long advance warning (hundreds of milliseconds), while cruising copepods are unlikely to sense remote particles by olfaction. However, the ability of copepods to remotely detect particles has only been observed once in freely swimming animals. Strickler (1982) reported that *Eucalanus pileatus* (2.6 mm) can perceive prey when the alga was 1.25 mm away or 430 ms before the alga reached the capture area. Unfortunately, information about the phytoplankton species in that study was not provided by the author, but Paffenhöfer and Lewis (1990) state that the copepod reacted to an incoming undisclosed larger alga. Using tethered animals, Koehl (1984) observed three

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individuals of *Eucalanus pileatus* (2.1 mm) to detect large dinoflagellates (*Gymnodinium nelsoni* [50 μm], and *Prorocentrum micans* [37 μm]) at a distance of 136 μm from the nearest appendage (i.e., at a much shorter distance than that reported by Strickler [1982]). Finally, Paffenhöfer and Lewis (1990) showed for the same species that the detection distance to 11 μm diatoms was much shorter, essentially only extending as far as the length of the setae of second antennae (A2) and maxillipeds (MXP). These studies suggest that the differences in detection distances might be related to differences in prey type (e.g., size, motility, etc.).

Many copepods face another problem in their sensory performance. They have low density and inevitably move upward when they feed. Their weak gravity anchoring (Emlet 1990; Tiselius and Jonsson 1990) limits the strength of their feeding current. The resulting short sensory core reduces the time between detection and capture considerably and requires very fast responses to capture any detected incoming cells—considerably faster than the advance detection times modeled for a hovering copepod (≈ 500 ms; Jiang et al. 2002). The few observations that exist on particle capture in small copepods are on tethered animals (Cowles and Strickler 1983; Price et al. 1983; Paffenhöfer and Lewis 1990) or on naupliar stages (Paffenhöfer and Lewis 1989; Bruno et al. 2012). None of these copepods displayed distant olfaction as reported by Strickler (1982), although distant detection of particles based on mechanoreception has been observed (Bundy et al. 1998). Landry (1980) showed that amputating the first antennae did not affect algal capture rates, suggesting that distant olfaction (Andrews 1983) was not likely even for a larger copepod (*Calanus pacificus*). These variable and partly contradictory results show that more studies are required for a better understanding of the detection and capturing of prey by planktonic copepods.

The general hypothesis of the present study was that prey are not detected remotely by the copepods *Paracalanus parvus* and *Pseudocalanus* sp. This hypothesis was tested through addressing the following specific objectives: (1) describing the detection and selection of prey by these copepods, and (2) determining the effect of prey size on detection distance and handling time. Additionally, we assessed the importance of sensory capabilities and handling time as limiting factors of food capture rates in copepods. We used high-speed, high-resolution video filming to investigate the capacity of the two copepod species to detect, capture, handle, and ingest or reject phytoplankton cells. *P. parvus* occurs mainly in the summer in temperate coastal water and feeds on small single cells or diatom chains. *Pseudocalanus* sp. has a wider temperature range and broader distribution, but feeds on similar prey as *P. parvus*. Our overall aim was to determine how prey cells are detected and potentially selected by these copepods. Our second aim was to examine whether the copepod food-capture rate is limited by sensory capabilities and handling times, or if the feeding is saturated at high food concentrations by other rate-limiting processes (e.g., gut passage).

Table 1. Mean equivalent spherical diameter (ESD \pm standard deviation (SD); μm) of the algae used in the experiments.

Algal species	ESD \pm SD (μm)	Abbreviation
Cryptophyte		
<i>Rhodomonas salina</i>	6.5 \pm 0.8	Rho
Dinoflagellates		
<i>Prorocentrum minimum</i>	11.2 \pm 1.2	Pmin
<i>Heterocapsa triquetra</i>	11.6 \pm 0.9	Het
<i>Oxyrrhis marina</i>	15.0 \pm 1.8	Oxy
<i>Scripsiella trochoidea</i>	15.4 \pm 2.1	Scrip
<i>Lingulodinium polyedrum</i>	20.9 \pm 1.6	Ling
<i>Protoceratium reticulatum</i>	24.1 \pm 2.5	Pret
<i>Akashiwo sanguinea</i>	32.7 \pm 3.4	Aka
Diatom		
<i>Thalassiosira weissflogii</i>	12.7 \pm 1.5	Tw

Methods

Filming of copepods was done on two occasions. For the first experiment, copepods were collected in the Gullmar Fjord on the west coast of Sweden during 27 October–29 November 2011 by gentle surface tows of a 50 μm plankton net. The cod end contents were diluted in surface water in the laboratory and the animals were used for experiments within 1–3 d. The second experiment was done during 03–12 September 2012 with copepods collected in the Gullmar Fjord on 31 August 2012.

One hour prior to filming, ~ 50 copepodites and adults were placed in the filming aquarium (50 mL clear plastic culture flasks; Falcon) filled with surface water and placed in a thermo-constant room at ambient surface-water temperature (9.5–11.0°C for the October–November experiment, and 20°C for the September experiment). Average prosome length of *Pseudocalanus* sp. was 0.65 ± 0.13 mm and that of *Paracalanus parvus* was 0.64 ± 0.10 mm. Just before filming, algae were added ad libitum either as single species or in mixtures. Phytoplankton used for the experiments are listed in Table 1. Algae were grown in batch cultures at 18°C and constant $120 \mu\text{mol m}^{-2} \text{ s}^{-1}$ photon flux using B1 medium.

Feeding behavior was video recorded at a frame rate of 2200 Hz by a Phantom version 210 (1280 \times 800 pixels) high-speed camera equipped with optics to yield a field of view of 5.7–76.5 mm². Collimated light was provided by a halogen bulb or by infrared lamp that was shone through the plastic culture flasks directly toward the camera. Algal captures and other behaviors that occurred in focus were stored. Prey positions at detection, appendage motions, handling time, and rejections were measured using ImageJ and Phantom software. Detection distance and handling time were recorded for a range of prey species (Table 1), and a more detailed analysis of the components of the feeding process was accomplished using *Heterocapsa triquetra* as prey. An algal cell was considered to be detected when at least one of the thoracic appendages deflected from its normal pattern of movement (Price and Paffenhöfer 1985), or when the swimming legs started to extend beyond their normal position. Detection distances

Table 2. Duration (milliseconds; ms) of components of feeding behavior of *Paracalanus parvus* (average \pm SD) with *Heterocapsa triquetra* as prey.

Activity	Duration (ms \pm SD)	n
A2 and MXP stroke	21.8 \pm 1.3	2
M2 stroke	10.3 \pm 2.2	7
Time for capture	35.1 \pm 19.3	12
Rejection time	61 \pm 21	6
Cleaning of A1	215 \pm 68	2
Cleaning of carapace	227	1

were measured from the center of the prey cell to the nearest feeding appendage, excluding the setae. Handling time was defined as the time between detection and rejection or ingestion. During this time, the copepod does not create a feeding current and cannot detect new prey.

Linear regression was used to test for effect of prey size on detection distance and handling time. Handling time was log-transformed to homogenize variances in the regression. All analyses were done using SPSS version 20 for Mac.

Results

Regular scanning mode—We found very similar results for the two species examined (*Paracalanus parvus* and *Pseudocalanus* sp.). Both displayed a highly regular motion of mouth parts to create a feeding current, which was mainly generated by the motion of the antenna (A2) and the maxilliped (MXP) in cycles of 21.4 ± 1.3 ms duration (Table 2). All other appendages moved in synchrony with this, except the swimming legs that were held more or less still. The water was moved past the ventral side of the copepod by synchronized beats of the A2, the mandible (MAND), the first maxilla (M1), and the MXP (Fig. 1). The exopod of the A2 extended up along the sides of the copepod and moved water along the side. The endopod of the A2, the exo- and endopods of the MAND, and the endopod of the M1 created the first part of the power

stroke, and the endopod of the MXP formed the second part of the stroke. A sequence for *Pseudocalanus* sp. has been selected to illustrate the generation of the scanning current (Fig. 2; [online Web Appendix, Video 1 \(www.aslo.org/lo/toc/vol_58/issue_5/1657a.html\)](http://www.aslo.org/lo/toc/vol_58/issue_5/1657a.html) Frames 1–87.)

Particle detection and capture—Most of the prey-capture events observed in *Paracalanus parvus* were initiated when incoming particles were within 50 μ m of the A2 or MXP, and we did not observe any remote detection (Table 3). Average detection distance was 35 μ m, and there was no significant effect of prey size (Fig. 3) (linear regression on log-transformed values, $p = 0.353$, $n = 95$).

When a particle was detected, the motion of the appendages changed according to where the particle was detected. During capture, the left and right appendages moved asynchronously to guide water containing the particle into contact with the M2 endopod or endite setae or the epipodite setae of the M1. Figure 4 shows the sequence of *Pseudocalanus* sp. motions leading to the capture of a *Heterocapsa triquetra* cell (see also movie in [online Web Appendix, Video 1, Frames 162–242](http://www.aslo.org/lo/toc/vol_58/issue_5/1657a.html)). The sequence starts at Frame 162 when the cell was detected, probably by the distal setae of the A2 endopod. Typically, the MXP and swimming legs were the first to show a capturing movement. Swimming legs started to move out and were fully extended at Frame 182. The A2, MAND, and M1 all made a recovery stroke (Frames 162–187). The MXP started a typical capture sweep when it moved in a wider circle (Frames 167–187); but in contrast to a regular stroke, the setae were trailing until Frame 187 when the stroke turned into an inward sweeping motion and setae moved water forward (Frames 187–202), meeting the tips of the MAND and M1. The opposite MXP (right) moved completely independently and 180° out of phase and helped pushing water toward the capturing area. This can be seen in Frames 177–182, where the right MXP was in the capturing area. A2 remained in a forward position (Frames 182–242) for the whole capturing event.

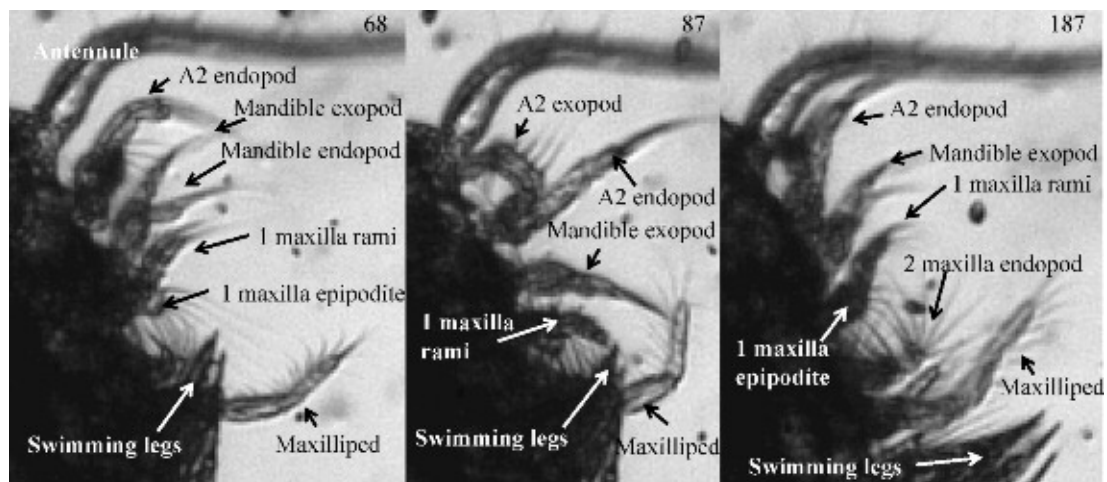


Fig. 1. Feeding appendages of *Pseudocalanus* sp. visible during different parts of the stroke cycle. Frames correspond to numbers in Figs. 2 and 4.

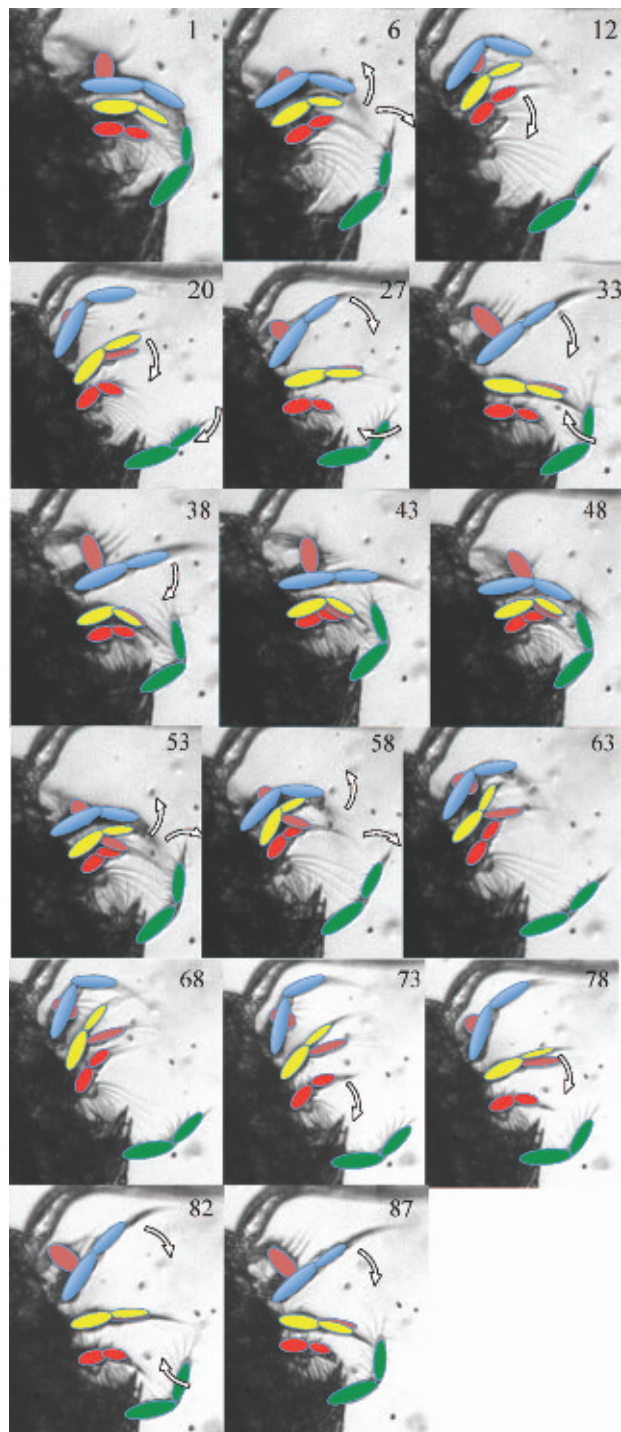


Fig. 2. Time sequence of normal scanning mode in *Pseudocalanus* sp. Frame number is shown and the position of A2 (blue), MAND (yellow), M1 (red), and MXP (green) are colored for clarity. The sequence starts with the recovery stroke (forward motion) of A2, MAND, and M1 and the power stroke (backward motion) of MXP (Frame 1). The A2 endopod moves forward and is bent backward along with the MAND and M1 rami (Frame 6). At Frame 12, the M1 starts its power stroke followed by MAND (Frame 27) and A2 (Frame 33). As M1 and MAND reach their most retracted position (Frame 43) the A2 lag behind (Frame 48), and at (Frame 53) the backstroke of M1 and MAND has already begun. The MXP moves 180° out of phase with the other

Table 3. Number of recorded detection events for the three main sensory appendages: the second antennae (A2), the first maxillae (M1), and the maxillipeds (MXP); and estimated capture time (milliseconds) from detection of the cell to the cell being at the mouth (average \pm SD).

	Encounter appendage			Capture time (ms)	n
	A2	M1	MXP		
<i>Paracalanus parvus</i>	6	2	4	35.1 \pm 19.3	12
<i>Pseudocalanus</i> sp.	7		1	31.1 \pm 23.4	8

A suction flow into the capture area was created by the simultaneous opening of the swimming legs (Frames 162–177), the rapid backward stroke of the MXP (Frames 176–172), and the recovery stroke of A2 and MAND (Frames 167–182). This capture area was bounded by the setae on the M1 epipodite and rami and by the endites and endopod setae of second maxilla (M2). The M2 endopod setae were very flexible and spread across a large area (Frames 177–182, 187, 212) and made short beats when trying to capture the cell. The M2 endopod and endite setae and the M1 handled the particle and brought it toward the mouth (Frames 217–242). During capture attempts, the M2 moved very rapidly with a cycle of 10.3 ± 2.2 ms (Table 2). The capturing event in Fig. 4 (Frames 162–242) thus consisted of 2 full cycles by the left MXP, 1–2 cycles in opposite direction by the right MXP, 3 sweeps by the M2, and somewhat unclear motions of the M1 and MAND. The cell disappeared at Frame 242 in the vicinity of the mouth. The capture of this cell lasted 36.4 ms and the average of all capturing events was 35 ± 19 ms (Table 2).

Handling time—During capture, handling, and rejection, the copepod was unable to capture other particles, and there was no feeding current created because the A2 did not perform any power strokes and the MXPs were involved in particle handling. Handling time in *Paracalanus parvus* varied between 10 ms and > 1 s and increased significantly with size of prey (Fig. 5).

Cleaning—Two types of cleaning were observed: cleaning of the antennule (A1), and cleaning of the carapace. Cleaning of A1 was observed frequently (Fig. 6; online Web Appendix, Videos 2 and 3). During A1 cleaning, the

←

mouthparts. It starts the power stroke at Frame 1 and twists its exopod such that a maximum surface is used for the stroke. At Frame 20, it has reached its maximum backward extension and the recovery stroke is started by twisting the exopod (Frames 12–27) such that the setae now point in the direction of the recovery stroke. The MXP exopod is also bent close to the body (Frame 33) and the tip is pointed into the parcel of water that is moved backward by the power stroke of the A2 (Frames 38–48). In this way, the water can be moved along the copepod even at the low Reynolds number that characterizes the flow pattern.

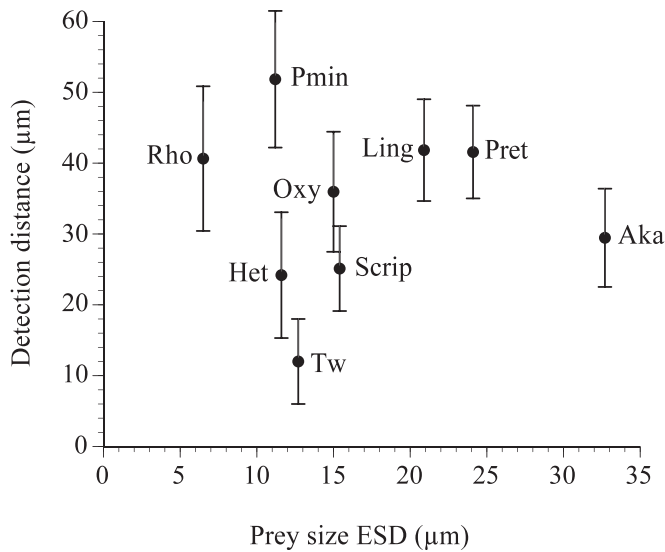


Fig. 3. Detection distances (μm , average \pm standard error) for *Paracalanus parvus* feeding on prey of different sizes. Detection distance is defined as the distance from the center of the prey cell to the nearest feeding appendage (excluding setae) at the time of detection. Prey sizes are given as equivalent spherical diameter (ESD). Prey species abbreviations from Table 1.

copepod folded the A1s along and beneath the side of the body. The MXPs were moved as far forward as possible outside other appendages and grabbed the A1. The MXP slid along the A1 (cleaning it), and at the same time the swimming legs moved backward along the A1. At the extreme backward position of the MXP, the A1 began to pull forward under the MXPs. As the A1 left the MXP, the swimming legs kicked forward (which moved the copepod slightly backward) and the A1s were extended. The entire procedure lasted 215 ± 68 ms (Table 2).

The cleaning of the carapace (online Web Appendix, Video 4) was performed by the A1s folding back and up over the carapace all the way to the front. The A1s were then moved over the entire carapace backward over the tail while the swimming legs were pointing straight down. After leaving the tip of the telson, the bent A1s unfolded and returned to their straight posture. Only one observation of this cleaning was recorded and it lasted 227 ms (Table 2).

Discussion

The present study is the first to film cell detection and capture by freely swimming *Paracalanus parvus* and *Pseudocalanus* sp. All behavioral responses were extremely rapid (0.02–0.2 s) and involved several appendages.

Detection—Detection of particles was accomplished by A2 and MXP, and upon detection particles were always very close to, or touched, the setae of these appendages. Remote detection was never observed. The capturing motion started when the particle was within the sweeping volume of the setae and in most cases the particle was within $5 \mu\text{m}$ distance from the setae. In line with this, Paffenhöfer et al. (1982) reported that the A2 of *Eucalanus*

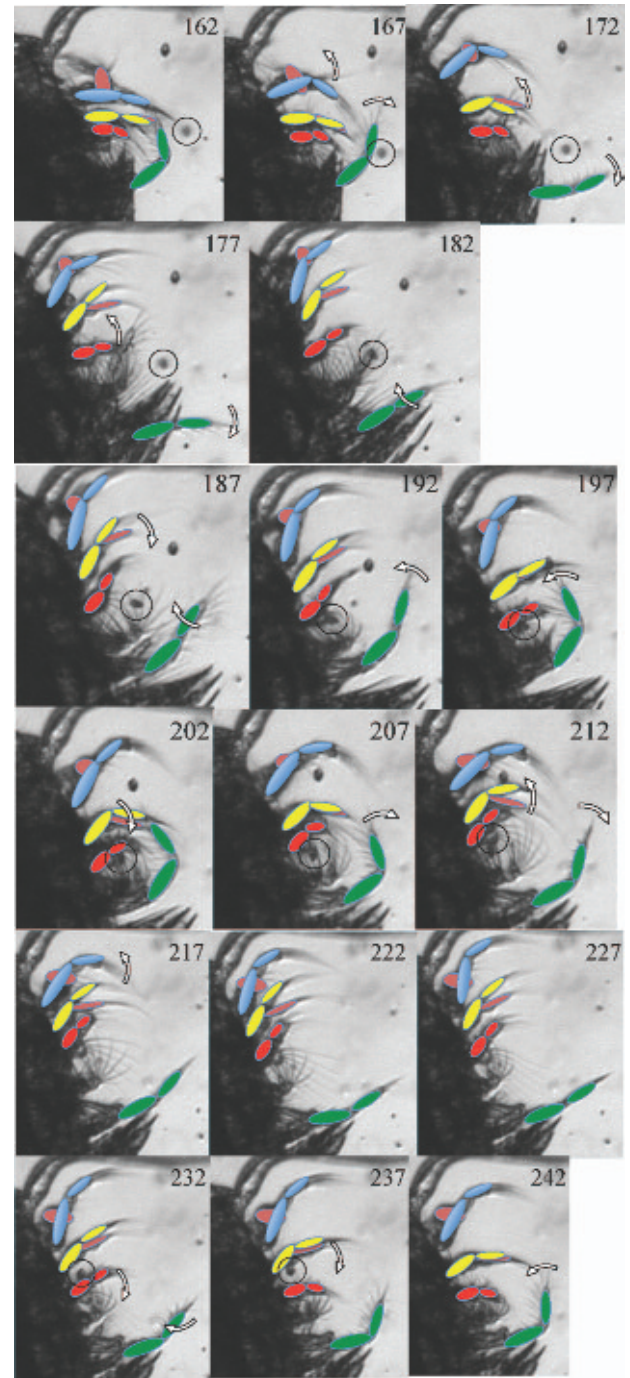


Fig. 4. Time sequence of the capture of a *Heterocapsa* cell (in circle) by a *Pseudocalanus* copepodite. Frame number is shown and the position of A2 (blue), MAND (yellow), M1 (red), and MXP (green) shown for clarity.

pileatus moved beyond an incoming particle, but no direct contact was seen. Price et al. (1983) showed for the same species that detected large cells (*Prorocentrum micans*, $50 \mu\text{m}$) were moved with the water parcel around the MXP, but were never in contact with the appendage. This is very similar to the detection and capture of phytoplankton prey described by Kjellerup and Kiørboe (2012) for a rapidly

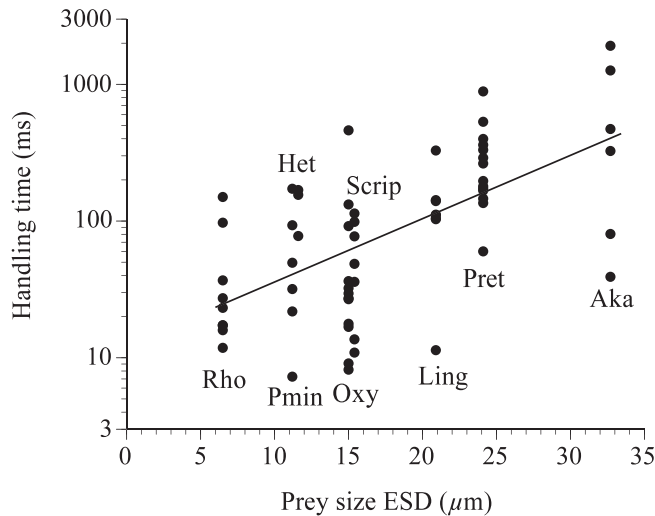


Fig. 5. Handling times (ms) from time of detection to the time when the cell leaves the appendages or when regular feeding motions commence in *Paracalanus parvus*. Regression line is $\log(\text{handling time}) = 0.046 \times (\text{prey size, } \mu\text{m}) + 1.08$, $n = 66$, $p < 0.001$.

cruising copepod, *Metridia longa*. High-speed filming by Paffenhöfer and Van Sant (1985) shows that single phytoplankton cells and fecal pellets were detected but that *E. pileatus* showed no reaction to 18 μm polystyrene spheres. Vanderploeg (1990) showed that larger plastic spheres (29–102 μm) were detected by *Diaptomus sicilis*, and Bundy et al. (1998) reported distant mechanoreception (0.48–1.41 mm) of 50 μm polystyrene spheres, although the feasibility of this has later been questioned (Visser 2001).

Chemical sensing or touch detection is the only way to perceive the cell if the flexible setae are involved. None of the setae have mechanoreceptors surrounded by scolopale (which are necessary for distant mechanoreception; Paffenhöfer and Loyd 2000), but the cells can be sensed when

touching the setae. Friedman and Strickler (1975) consider the setae as sensillae with numerous pores in the distal parts and that the setal wall is different from the thicker basal portion of the setae. Bimodal sensilla are concentrated in the mouthparts and are involved in the close-range location and evaluation of food that occurs during handling of prey (Hallberg and Skog 2011).

Previous to our study, the only other rigorous testing of perceptive distances was done by Paffenhöfer and Lewis (1990). They determined the distance from the tip of the A2 and MXP of *Eucalanus pileatus* females to an incoming *Thalassiosira weissflogii* cell (11 μm) when the first sign of irregular motion of any appendage appeared. Distance of cell perception varied between 200 μm and 340 μm from the tip of A2 and 220 μm and 460 μm from the MXP. The distance is similar to the average length of the setae, 200 μm and 320 μm , for the A2 and MXP, respectively; and hence, cells were very close to the setae when detected. Thus, gustation or mechanoreception within the sweeping volume of the A2 and MXP is the most likely detection mechanism. Paffenhöfer and Lewis used tethered animals in their observations, which precluded any correction of the body position in relation to prey (Strickler 1982).

Capture—The capture by *P. parvus* always started with a wide sweep by the MXP (Fig. 4; Frames 172–187). This single, high-amplitude motion was also shown in Price et al. (1983). All the cells used as prey in our study were larger than the spacing between setae of the endites of the M2, and they were all captured actively as opposed to passive capture of small cells (Price et al. 1983). The cells were therefore handled by different appendages when they were moved into the capture area. The endite and endopod setae of the M2 (Fig. 4; Frames 187 and 217) and the epipod setae of the M1 (Fig. 4; Frames 217 and 222) were active in handling the cells. The motion of the M2 was also

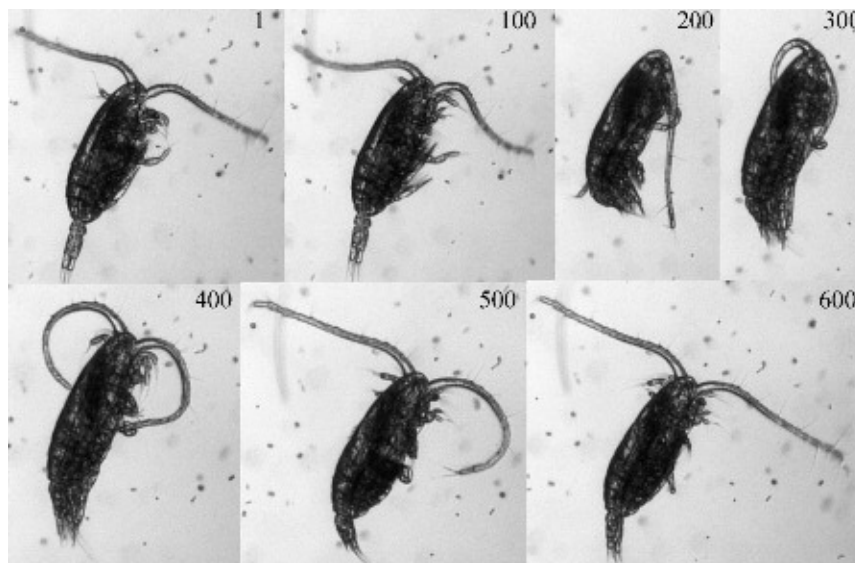


Fig. 6. Cleaning of the antennules by *Paracalanus parvus*.

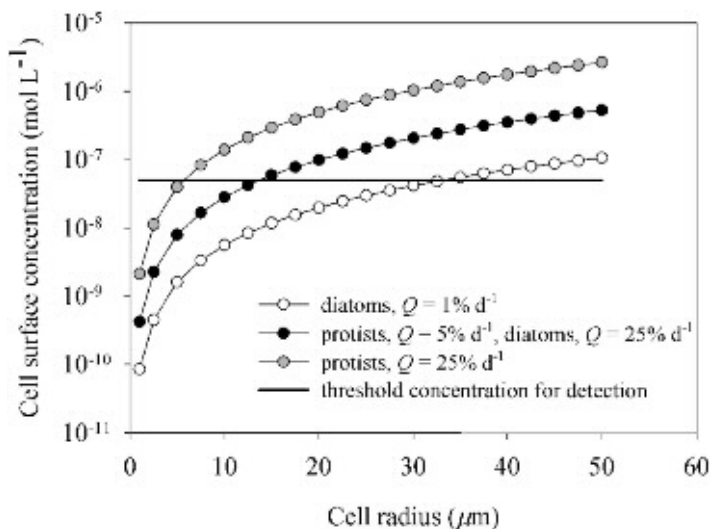


Fig. 7. Estimated cell-surface concentration of amino acids for diatoms and other protists as a function of cell size. Leakage rates (Q) are $1\% \text{ d}^{-1}$ for diatoms and $5\% \text{ d}^{-1}$ for other protists. For comparison, hypothetical high leakage rates of $25\% \text{ d}^{-1}$ are also shown. Horizontal line indicates threshold concentration for chemosensory detection of copepods.

decoupled from the other appendages and it moved at twice the frequency to bring the cell toward the mouth.

Limitations to olfaction—The model of distant olfaction in the detection of prey cells by feeding-current feeding copepods assumes that chemicals leak out from the prey particle fast enough to yield detectable concentrations at some distance from the cell surface. Legier-Visser et al. (1986) made calculations and suggested that likely leakage rates for a rapidly growing phytoplankton cell of $50 \mu\text{m}$ diameter would be insufficient. We here expand on their model to examine the effect of cell size. The concentration of organic solutes in the phycosphere of a spherical phytoplankton cell (C_r) in still water and as a function of the distance to the cell center (r) depends on the rate at which solutes leak from the cell (Q , mol s^{-1}), on the diffusivity of the solutes (D , about $10^{-5} \text{ cm}^2 \text{ s}^{-1}$ for small biological molecules), and on the radius of the cell (a ; Kiørboe 2008):

$$C_r = \frac{Q}{4\pi Dr} \text{ for } r > a \quad (1)$$

If the threshold concentration for chemical detection is C^* , then this cell can only be detected chemically if the concentration of solutes at the surface of the cell, C_a , is larger than the C^* , and the detection distance, R , is

$$R = \frac{Q}{4\pi DC^*} \quad (2)$$

If the cell is arriving toward a copepod in an accelerating, sheared feeding current, then the phycosphere is stretched and the detection distance extended. Jiang et al. (2002) calculated the stretching of the phycosphere and the potential detection distance (and lead time) for a phytoplankton cell of $25 \mu\text{m}$ radius, and made implicit

assumptions of the magnitudes of Q and C^* by assuming that $R = 10 \times a$. With this assumption, remote chemical detection at a distance of about one body length would be possible for a small, hovering or slowly cruising copepod and consistent with the empirical report of Strickler (1982).

What are the likely magnitudes of Q and C^* for a phytoplankton cell and a copepod, respectively? Leakage rates for phytoplankton cells have been measured repeatedly; they are often expressed as a fraction of the carbon fixation rate, and a recent study examining a large range of phytoplankton species estimated an average value of $2\% \text{ d}^{-1}$ (López-Sandoval et al. 2013). However, it is more relevant to express Q as a fraction of the cell content (Bjørnsen 1988). Bjørnsen (1988) estimated the likely magnitude of Q to be about $5\% \text{ d}^{-1}$ of the cell mass for phytoplankton, consistent with observations. We combined the carbon:nitrogen ratios (~ 5) and the carbon:cell volume relations of Menden-Deuer and Lessard (2000) for diatoms and all other protists (the two groups vary by a factor of 5 in C- and N-density), assumed that all leaking material would be amino acids, and assumed that the N-content of amino acids of an average molar weight of 112 is 16%. We finally assumed $C^* = 5 \times 10^{-8} \text{ mol L}^{-1}$, because the threshold concentration must exceed the background concentration of amino acids in the ocean (10^{-7} – $10^{-9} \text{ mol L}^{-1}$; Mopper and Lindroth 1982; Poulet et al. 1991; see also discussion in Kiørboe and Thygesen 2001).

The minimum requirement for chemical detection is that the cell-surface concentration exceeds the detection limit. The calculations demonstrate that there is a minimum cell size for chemical detection (Fig. 7). Signals generated by smaller cells dissipate by diffusion too rapidly. The estimated minimum size is about $35 \mu\text{m}$ radius for diatoms and about $15 \mu\text{m}$ for other protists. If leakage rates are higher or detection limits are lower than assumed above, smaller cells can be detected. The predictions are consistent

with our observation of detection distances of $< 50 \mu\text{m}$ for the cell sizes that we tested (equivalent spherical diameter 7–33 μm).

Distant detection, as observed by Strickler (1982) and proposed by Andrews (1983) and Moore et al. (1999), is only feasible for cells larger than those estimated above. Only unusually large and leaky protists may fulfill the assumptions of Jiang et al. (2002). We conclude that nearby chemical detection is feasible for prey cells with a radius $> 10\text{--}15 \mu\text{m}$, but that distant detection as observed by Strickler (1982) and by the mechanism of Andrews (1983) is possible only for very large and unusually leaky cells.

Dual receptors—The presence of both mechano- and chemoreceptors in the setae (Paffenhöfer and Loyd 2000) show their dual action as near-field chemoreceptors and as manipulating appendages after food detection. Our observations show that only when cells were within a few cell diameters from the distal parts of the A2 and MXP did the animal detect them. Cells were always detected within the volume swept by the rapidly moving distal setae of the A2 and the MXP and often during the back-stroke of the A2. The rapid motion of the setae will reduce their diffusive boundary layer. Because molecules from the prey cell have to diffuse through the diffusive boundary layer of the setae to be detected, this reduces the time for detection. The time to diffuse through this layer is $\sim L^2/6D$, where L is the thickness of this layer. Because the diffusion time scales with layer thickness squared, any thinning of this layer will speed up the process dramatically. Jiang et al. (2002) arrived at a similar conclusion that rapid beating of sensory appendages should facilitate encounters between individual molecules of the chemical signals and chemoreceptors.

The cell is brought closer to the appendages surrounding the capture area; therefore, the signaling will shift to gustatory (taste) and mechanical. To handle the particle, the copepod needs to touch it and move it toward the mouth. This can be accomplished because the setae of the MXP, A2, and MAND all have both chemosensory and mechanosensory function (Paffenhöfer and Loyd 2000). The numerous chemo-sensors and contact mechano-sensors make the appendages ideally suited to handle the detected cells.

Feeding saturation—The limiting factor for repeated captures in a short time is the handling time. During this time, the feeding current is stopped because the A2 does not create strong power strokes. The maximal number of cells that were ingested by *Paracalanus* spp. in experiments with mixtures of *Isochrysis galbana*, *Thalassiosira weissflogii*, and *Rhizosolenia alata* were 45, 42, and 0.36 cells ingested copepod $^{-1} \text{ min}^{-1}$, respectively (Paffenhöfer 1984). This translates to a combined handling time of 687 ms per cell, well above the handling times of 24–385 ms shown by our recordings (Fig. 5). The conclusion is therefore that the detection and capture of particles is not the limiting factor for feeding rate, but that (1) the quality of particles (should they be ingested or rejected?), (2) the concentration of particles, and (3) the gut evacuation time and the degree of

pellet packaging are the limiting factors for the feeding in copepods. Paffenhöfer (1984) similarly found no reason to believe that handling time limits intake. The saturating factor in the functional response is the digestion and gut transit time of ingested particles, and there is ample time for tasting and rejecting particles of low nutrient value. Small coastal copepods are confronted with a wide range of potential food particles, many of them with limited nutritional value. The evolutionary advantage of a short handling time under those circumstances is that more time is available for tasting, and fewer low quality particles will be ingested and less energy will be spent on digesting inferior food. The selective capability is tuned toward rapid assessment of the quality of frequently encountered particles.

Food-web implications—Small cyanobacteria (1 μm) dominate the marine primary production in vast areas of the ocean (Agawin et al. 2000). These small cells are eaten by non-selective grazers (such as tunicates and flagellates) that rely on advection-diffusion for prey encounter. The chemical signals released by such small cells are too weak and dissipate too rapidly to constitute a basis for prey selection, and no olfactory or gustatory detection is possible (Jackson 1987). Larger protists contribute less to global primary production, but their size allows for prey selection based on chemical composition and nutritional value (Huntley et al. 1983), as demonstrated here and confirmed by incubation studies (Cowles et al. 1988). The selective capability of copepods feeding on these larger prey is of importance. The resulting trophic upgrading of, for example, essential fatty acids, is significant (Tiselius et al. 2012), and copepods constitute one of the critical shunts of essential fatty acids and lipids to higher trophic levels in marine food webs. The species studied here never use ambush or cruising mode to capture prey, but rely on their feeding current to bring prey within reach of capture. This feeding mode is suitable for relatively abundant prey of small size and limited motility, which are common in coastal waters.

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